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VIII.—*On the Homology of the Buccal Parts of the Mollusca.*
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[Plate VI.]

THE oral organs have, throughout the animal kingdom, furnished some of the most important systematic characters. Linnæus first based the system of Mammalia, and Fabricius that of Insects, upon the structure of these parts. It was, however, not until 1847 that Prof. Lovén* placed the natural classification of the Mollusca on a scientific base, chiefly founding it on the dentition of the tongue (radula). Another part of the oral organs, the mandibles, has been much neglected. Most authors understand by this name all hard bodies near the entrance of the mouth. I believe it is necessary to distinguish two (or perhaps three) different kinds of oral plates corresponding to the mandibles and maxillæ of the Arthropoda. The maxilla is a median, unequal-sized, corneous plate attached to the bulbus pharyngeus over the oral aperture, and serving to divide the food into morsels. It is found in all Land Pulmonata (Phyllopora, Gray). According to its structure, I have distinguished the following groups:—*Oxygnatha*, with a smooth maxilla; *Aulacognatha*, with a closely sulcated maxilla, crenulated at the edge; *Odontognatha*, with a strongly ribbed maxilla, forming projecting teeth on the edge; *Gonio-gnatha*, with the maxilla composed of oblique plates (genus *Orthalicus*)†. Among the Land Pulmonata, the maxillæ are wanting in the *Agnatha* (Vermivora, Gray), which swallow their prey entire and alive (genera *Onchis*, *Testacella*, *Helicophanta*, *Caffra*, *Daudebardia*, *Streptaxis*, *Urocoptis*, *Glandina*). Among the marine Mollusca, it is only found in *Ægirus* and, perhaps, *Siphonodentalium*.

* Öfversigt af Kgl. Vetenskaps Akademiens Förhandlingar, 1847.

† Mörch, Malacozologische Blätter, 1859.

The maxilla of the aquatic Pulmonata is provided with a lateral, linear, moveable appendage on each side, the real homology of which is not yet quite ascertained, nor even whether it is a part of the maxilla or independent of it.

The maxilla is divided into two* in the case of the young *Limax* before it leaves the egg. The two halves are afterwards united by an intermediate piece, which, in a more advanced period of growth, is indicated by a notch in the projecting middle tooth. I do not believe this circumstance shows that the maxilla is formed by a union of the lateral mandibles.

A superior and inferior maxillæ are only found in the Cephalopoda, and perhaps in the larval state of some Pectinibranchiata; but it is not placed beyond doubt that the beak of the Cephalopod is really homologous with the maxilla in the Pulmonata. The maxilla of *Succinea* is not unlike the upper maxilla in the Cephalopoda. Prof. Van Beneden's figure of the "mâchoire supérieure et inférieure" of *Amphipeplea glutinosa* (Exercices Zootomiques, f. 6-9) looks very like the beak of a Cephalopod; but it may be erroneous, because the radula is represented (f. 7) as forming a part of the lower maxilla. A similar mistake was committed by Moquin-Tandon, who represented in *Neritina* as superior and inferior maxillæ what, according to Claparède, are only the edges of a corneous membrane lining the oral cavity.

Messrs. Alder and Hancock have shown, in *Acanthodoris pilosa*, a solitary inferior maxilla represented by a flat plate with a split in front protruding from the mouth; but this part seems to me more likely to belong to the lingual cartilages.

Perhaps the "anterior or lower lip, armed with teeth," represented by Macdonald† in *Clio caudata* is the edge of an inferior maxilla.

The *mandibulæ* are two lateral concave plates, not unlike a bivalve shell‡, the free edge of which (masticatory edge § of Bergh) is either tuberculated or denticulated. From the position of the muscles and from the form of the pectinated edge in *Phyllodesmium*, Ehrb. (Bergh, 'Anatomie'), it appears that the mandibles cannot be used for mastication, but are only adapted for use as a pair of forceps to hold the food during the triturating action of the radula. By the umbones of the mandibles (umbilicus, Midd., Bergh) the two halves are united with muscular ligaments. This kind of lateral mandibles is found in the Pleurognatha Gymnibranchiata (*Æolidiæ*, *Diphyllidiæ*, &c). In

* Heynemann, Malacozoologische Blätter, 1861, p. 143. The same is the case with *Vitrina* in its young state.

† Trans. Royal Soc. Edinb. vol. xxiii. pt. 2. p. 188, t. 9. f. 3.

‡ Described as such by Brown in *Binghamia paradoxa*.

§ Cutting edge (Alder and Hancock).

Proctonotus mucroniferus Alder and Hancock have discovered a "corneous transverse arch or strap" uniting the two halves, and reminding us of the middle maxilla in the Pulmonata. The nature of the mandibles described by Troschel (Gebiss der Schnecken, t. iii. f. 18) in *Pneumodermon* is, in my opinion, very doubtful.

The *cheek-plates**, or immoveable mandibles, are two lateral plates, without cutting edges, composed of scaly or acicular † particles, which seem only of use to protect the inside of the mouth from injury by the spinous tongue. Sometimes the two plates are united above by a ligament. This kind of mandible is found in nearly all the *Tenioglossata*, as well in those provided with a *rostrum* (*Cyclostomus*, *Valvata*, *Rissoa*, *Jeffreysia*, *Crepidula*, *Vermetus*, *Trichotropis*, &c.) as in those with an *haustellum* (*Marsenia*, *Natica*, *Cypræa*, *Cassis*, *Triton*, *Strombus*, &c.): vide Troschel, Gebiss der Schnecken. These plates are apparently wanting in all the *Rhachiglossata* (*Murex*, *Fusus*, *Nassa*, &c.). The linear horny plates described in *Buccinum undatum* by Cuvier (Anat. des Mollusq. figs. 11, 12) and by Valenciennes (Archives du Muséum, t. v. p. , t. 25. f. 6) are probably appendages of the tongue, and used as a handle in perforating the shells on which they prey.

The *prehensile collar* (Hancock) is a circular band composed of conical, often forked, erectile spines. Sometimes it is entire, as in *Ancula cristata* and *Goniodoris nodosa*; in others it is divided into two lateral parts, not unlike cheek-shields, as in *Idalia pulchella* and *Acanthodoris pilosa*.

Evertile cheek-cushions ("lames latérales," Lacaze-Duthiers ‡), two large evertile lateral sacs, covered with close-set lanceolate plates, like pavement, in *Pleurobranchus*. They seem to be an intermediate form between the prehensile collar and the evertile arms of the Gymnosomata and Cephalopoda.

Cheek-hooks or *cheek-crooks* (harpagæ §); mandibles, Eschricht, in *Clione*; "les cæcums de la bouche, avec un tube corné dans l'intérieur" (Van Beneden ||); "evertile tubes serving as prehensile organs" (Troschel ¶) (this author has not detected these organs in *Clione* and *Pneumodermon*); "lateral or cheek-pouches" (Macdonald**. Eschricht †† first showed that these tentacle-

* "Mandible-like parts, indumentum epitheliæ, the horn sheaths of the inner lip" (Bergh).

† In Thecosomata (*Hyalæa*, &c.) they are composed of four or five band-like plates (vide Troschel, Gebiss).

‡ Ann. des Sc. nat. sér. 4. vol. xi. t. 7. f. 4.

§ I intentionally use this form of the word.

|| Exercices zootomiques.

¶ Gebiss d. Schn.

** *Loc. cit.* and Linn. Trans. xxii. 1858, p. 248.

†† Anatomiske Undersøgelser over *Clione borealis*, 1838.

like organs, which are always provided with corneous hooks, are evertile; but this has been established by Eydoux and Souleyet* in the genera *Pneumodermon* and *Clione*.

The long arms of the decapod Cephalopods seem to me without doubt the same organs as the cheek-hooks of Gymnosomata; they have the same latero-ventral position, and are retractile within a cavity or pouch inside the short arms, which may be considered as a single fissured veil, and perform the same function in the animal. Prof. Lovén considered the long arms of Decapoda homologous with the tentacula (vibracula) of the Gasteropoda, and compared them specially with the rhinophores of *Doris*. I do not believe that this homology is natural, because the tentacula are always dorsal, and the "long arms" of Cephalopoda always latero-ventral. It seems also very doubtful whether an organ of prehension can be homologous with an organ of smell. If the Cephalopoda have no tentacula at all, the "crêtes auriculaires" (D'Orb.) or "paupières inférieures" (D'Orb.) of the Myopsid Decapods may be considered as their homologue. The triangular filaments over the eyes of *Octopi* are perhaps, too, a form of tentacula. I believe they are provided with a nervous ganglion at their base, like those of *Doris*.

The "organe en pioche," in *Conus*, of Quoy and Gaimard is a tubular sac, provided with arrow-like corneous hooks with a hollow channel, which are considered venomous. I have had an opportunity of confirming the exactness of the anatomy represented in the 'Voyage de l'Astrolabe.' As these hooks are not situated in the true oral tube, it is still very doubtful whether they really can be considered to belong to the radula. I suppose these arrow-like hooks are more allied to the cheek-hooks of Gymnosomata. As the hooks turn their points in opposite directions in the two arms of the pouch, it is probable they are evertile each in a different direction, but how and through what aperture is not yet discovered.

On the Palpi and Lips.

There are often in the Gasteropoda two different apertures in the same animal, called mouths. The true mouth is the anterior opening of the bulbus pharyngeus, frequently prolonged into an haustellum. This opening is only provided with the hard plates described above. The outer or false mouth is a simple slit in the skin, containing the lips or palpi, but never any mandibles; and it forms a passage for the protrusile haustellum, which, in a retracted state, is concealed in a cavity behind this slit.

In the Acephala the palpi are represented by two pairs of

* Voyage de la Bonite; Mrs. Gray's figures of Moll. t. 255. f. 3.

foliaceous expansions, grooved (sulcated) inside, and destined to conduct the particles of food to the mouth, and they may thus be considered passive prehensile organs.

In the Calyptræidæ the same organ is composed of a single pair, which is represented in all drawings of these mollusks as two intertentacular tubercles. In reality these tubercles are flat inside, grooved as in the Acephala, and probably used as a pair of forceps, as appears from their relative position in different specimens. In *Capulus* the palpi form a long haustellum-like tube, with a narrow slit on the upper side. In *Dentalium* and *Siphonodentalium* they form a closed, flat tube.

In the *Doridæ* the palpi are situated near the outer oral aperture, and are sometimes of a linear form, with a longitudinal groove on the middle, sometimes foliaceous (*Hexabranthus*) or meeting together in a semicircle (*Lamellidoris*), or they become the oral veil.

In *Conus*, *Terebra*, and perhaps *Pleurotoma* this veil is developed into a large infundibuliform sucking-cup, which disappears when the haustellum is protruded. This veil was for a long time regarded as the proboscis, until Dr. Gray* showed its real nature. In *Conus tulipa* and *C. striatus* the edge is divided into many digitations. (Voyage de l'Astrolabe; Mrs. Gray's figures, i. t. 10. f. 6, and 12. f. 2.)

In the gymnosome Pteropoda the oral veil is divided into several conical "arms," provided with numerous suckers, and probably corresponding to the grooves in the labial palpi of Acephala and Calyptræidæ.

In the Cephalopoda these "arms" are still more developed, and united by a membrane, which sometimes extends to the tips (*Cirroteuthis*, Eschricht).

Under the name "velum," as employed by Lovén, very different organs are confounded. I believe three kinds may be distinguished:—

1. The *oral veil*, formed by the palpi or lips, an organ for prehension or locomotion (Cephalopoda, larva of Opisthobranchia, e. g. *Doris*), or even partly available as a male organ (hectocotyl of the Cephalopoda), as in the Spiders. The "membrane orale" of D'Orbigny, found in the decapod Cephalopoda, seems to me a kind of suspensorium, like the "brids" of the funnel.

2. The *tentacular veil*, situated further from the mouth. It is placed, in *Pleurobranchus*, above the mouth, and formed by the union of the anterior tentacula (vibracula in *Aplysia*). In

* "On the Head of the genus *Conus*," Ann. Nat. Hist. Aug. 1853, p. 176.

Clione its two halves can cover the arms entirely, like a hood (see Eschricht's 'Anatomie'), and resemble the "crêtes auriculaires" and "paupières inférieures" of D'Orbigny, above mentioned.

3. The *post-tentacular veil* is only found in the larval state of *Rissoa*, Lovén (Öfversigt, 1847), and in the genera *Chiropteron* of Sars* and *Macgillivrayia* of Macdonald.

In analogy with the names of the foot given by Prof. Huxley, these three kinds of velum may be called Prohision, Mesohision, and Metahision.

That the short arms of Cephalopoda cannot be considered the homologue of the foot, is evident from the circumstance that the same kind of arms is found in the Pteropoda Gymnosomata simultaneously with an undoubted foot. Prof. Lovén first showed that the *funnel* must be the foot of Gasteropoda, and he suggests that the interior *valvula* of most Decapods and of *Nautilus*† corresponds to the solea pedis of Gasteropoda—a proposition which, I believe, is correct. The funnel would thus correspond to the epipodium in the Gymnosomata; its dorsal wings, attached to the neck of nearly all Decapod Cephalopoda, are provided with three cartilages which may be compared to a tripartite operculum‡, thus proving that the lobus operculigerus of Lovén§ is a part of the epipodial line (Huxley), and not of the true foot (solea).

Pedipes afra, as represented by Adanson (Hist. Nat. du Sénégal, tab. 1) and by Lowe (Zool. Journ. vol. v. pl. 13. f. 8, 9), is the only example of a foot divided into the *propodium*, *mesopodium*, and *metapodium* of Prof. Huxley.

EXPLANATION OF PLATE VI.

Fig. 1. *Pneumodermon*: intestinal channel, with the labial suckers, salivary glands, stomach, rectum, and anus. The cheek-pouches are united at their ends by a muscular band.

Fig. 1b. The cesophagus opened, to show the entrance of the cheek-pouches, with the prehensile hooks in the centre, on both sides of the radula.

* *Chiropteron semilunare*, Sars (Beskrivelser og Jagttagelser 1835, t. 14. f. 38), is probably the larva of *Aporrhais*.

† R. Owen, 'On the Pearly Nautilus,' t. 3. f. 2 e.

‡ The middle cartilage is articulated to the inside of the front of the shield or dorsal plate, and the two lateral cartilages to similarly excavated plates in the inner margins of the mantle.

§ The dorsal part of the metapodium (Huxley, "On the Morphology of Cephalous Mollusca," Phil. Trans. 1853, p. 29).

Fig. 1c. *Pneumodermon*, with everted prehensile hooks (harpagæ). (Figs. 1, 1 b, and 1 c from 'Voyage de la Bonite.')

Fig. 1 d. One of the sacs opened, to show the evertile hooks, with some detached corneous spines. (From Van Beneden's 'Exercices zootomiques.')

Fig. 2. *Clione limacina*, Phips.: the anterior part of the œsophagus. The harpaga of the right cheek-pouch is everted; the left retracted, and seen through an opening.

Fig. 2 a. The harpaga, with from 24 to 32 corneous hooks. From Eschricht's 'Undersøgelse om *Clione borealis*.'

Fig. 3. *Onychoteuthis*, from the ventral side, with protruded arms. It is doubtful whether the metacarpal suckers are really destined to act against each other, as represented by Férussac and D'Orbigny.

Fig. 4. *Conus tulipa*: the oral veil expanded at the edge, and opened to show the haustellum.

Fig. 4 a. The oral veil in a contracted state.

Fig. 4 b. The intestinal channel and its glands, the two liver-lobes, and an intermediate small so-called "gland," perhaps the true stomach. Over the nervous ring is the "organe en pioche," attached to the œsophagus by muscular bands; but I have not been able, in a specimen of *C. consors*, to discover any communication with the interior of the œsophagus. It cannot, therefore, represent the papillæ of the tongue, which in *Littorina* and *Patella* are of enormous length. At the insertion of the "organe en pioche," close to the base, is the long vermiform canal of the single "glande salivaire cucumiforme." The walls of this cylindrical organ are enormously thick and muscular; and it therefore seems to me not to be a salivary gland, but a suctorial stomach, like that of most haustellate insects. A similar unequal sac, in the same position, is found in the following Mollusca, all of which are provided with an haustellum:—

Murex cichoreus, Voyage de l'Astrolabe, t. 36. f. 1, et Suppl. t. 2. f. 1 d, troisième glande salivaire.

Dolium olearium, ibid. t. 41. f. 4.

Voluta fusus, Q. & G. ibid. t. 44. f. 9 h, "diverticulum ou cæcum œsophagien très-considérable;" and f. 10 and 11.

Ancillaria albisulcata, ibid. t. 49. f. 11 d, "diverticulum, espèce de cæcum."

The petiolate cheek-pouch in *Lamellidoris*, described by Mr. Hancock, is perhaps, too, a kind of instrument destined to produce a vacuum, like the suckers of Cephalopoda.

Fig. 4 c. The "organe en pioche" opened, to show the arrows turning the points in a different direction in each branch.

Fig. 4 d. Different forms of the arrows, hollow inside.

(Figs. 4-4 d from 'Voyage de l'Astrolabe,' t. 44.)

Fig. 5. Pharynx of *Pleurobranchus*, showing the "lames latérales" on both sides of the tongue. a. The hard parts of the "lames latérales," strongly magnified. (From Lacaze-Duthier's 'Anatomie du Pleurobranche orange,' l. c.)